Smarter through group living: A response to Smulders

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Abstract

In our recent paper(Ashton, Ridley, Edwards, & Thornton, 2018) we investigated the causes of individual variation in cognitive performance in the Australian magpie *Cracticus tibicen dorsalis*. We presented individuals with a cognitive test battery consisting of four tasks designed to quantify behavioural inhibition, associative learning, reversal learning, and spatial memory. We reported a strong, positive relationship between group size and individual performance in all four tasks of the cognitive test battery(Ashton, Ridley, et al., 2018). Furthermore, females that performed better in the cognitive test battery had greater reproductive success (a greater number of successful clutches per year, fledglings per year, and fledglings surviving to independence per year), compared to females that performed badly (Ashton, Ridley, et al., 2018). An opinion piece by Smulders (2018) raised the interesting notion that these patterns may be underlined by motivational factors. In this commentary we highlight why none of the available data is consistent with this explanation, but instead support the argument that the demands of group living influence cognitive development, with knock-on consequences for fitness.

Key words

Social intelligence hypothesis, cognitive ecology, Australian magpie

In the last few years the field of cognitive ecology has increasingly begun to recognise the importance of adopting an intraspecific approach, focusing on the causes and consequences of individual variation in cognitive performance(Ashton, Thornton, & Ridley, 2018; Boogert, Madden, Morand-Ferron, & Thornton, 2018; Morand-Ferron, Cole, & Quinn, 2015; Thornton & Lukas, 2012). A number of important recent advances have been made in the field, including the identification of links between cognitive performance and group size(Ashton, Ridley, et al., 2018; Langley, Horik, Whiteside, & Madden, 2018), effects of spatial memory on survival (Maille & Schradin, 2016) and evidence for a "general cognitive factor" underpinning performance across a range of tasks in birds (Shaw, Boogert, Clayton, & Burns, 2015). However, determining that observed differences in individual performance result from cognitive differences rather than other factors is extremely challenging (Boogert et al., 2018; Rowe & Healy, 2014; Thornton, Isden, & Madden, 2014), so the results of these studies need to be interpreted with great caution. This is particularly the case where studies are carried out on wild populations of animals, where results are often correlational because experimental manipulations may be logistically challenging, or (in some cases) impossible. In our work on Australian magpies, for instance, experimental manipulations of group size were neither logistically or ethically feasible, so a causal effect of group size on individual cognitive performance could not be determined unequivocally. Nevertheless, we took great pains to rule out alternative explanations for the observed relationship.

Smulders (2018) suggests individuals living in larger groups may face greater competition for food, and therefore have greater motivation to interact with experimental tasks, which may explain the positive relationship between group size and cognitive performance reported in our study (Ashton, Ridley, et al., 2018). First, we note that a positive association between group size and food competition is by no means a universal phenomenon; indeed several studies show that foraging intake can increase with increasing group size (Blundell, 2002; Courchamp, Rasmussen, &

Macdonald, 2002; Sorato, Gullett, Griffith, & Russell, 2012). More specifically, several lines of evidence suggest differences in motivation do not underpin the group size- cognition relationship in Australian magpies. We examined the potential effect of two factors likely to influence food motivation: body mass and foraging efficiency (defined as the mass of food (in grams), caught per foraging minute (Edwards, Mitchell, & Ridley, 2015)). Less efficient foragers (who might be predicted to be hungrier), and individuals in poor condition (potentially indicated by body mass), might be more motivated to engage with the tasks and therefore perform better. Neither of these factors predicted cognitive performance (Ashton, Ridley, et al., 2018). Furthermore, additional analyses show there was no relationship between foraging efficiency and group size (Spearman's correlation, $r_s = -0.097$, $p = 0.458$, $n = 61$ individuals across 14 groups ranging in size from 3 - 12), suggesting there is no difference in food competition between groups of different sizes. Although food motivation is expected to vary over time in response to prevailing conditions, we found that individual cognitive performance was highly consistent, with individuals showing strong repeatability when tested on different versions of each task (Ashton, Ridley, et al., 2018). We also examined the potential effects of factors that may be direct indicators of food motivation, namely the latency to interact with the task, and time spent interacting with the task ("task attention"). One would expect more food motivated birds to approach the task more quickly and spend more time engaged with the task; if our results were driven by food motivation, we would therefore predict latency to interact with the task and time spent interacting with the task to explain variation in cognitive performance. However, neither of these factors predicted cognitive performance (Ashton, Ridley, et al., 2018). For these reasons, differences in motivation are unlikely to drive the positive relationship between group size and cognitive performance.

Repeated testing of juveniles showed that the relationship between group size and cognitive performance emerged after 100 days post-fledging (Ashton, Ridley, et al., 2018), consistent with the idea that the size of the group an individual grows up in has an influence on its cognitive development (we note that at day 100 it was only possible to quantify performance in behavioural

inhibition and spatial memory because fledglings at this age were unable to pass the associative and reversal learning tasks, regardless of their group size (see methods, Ashton, Ridley, et al., 2018)). Smulders (2018) suggests motivation may also explain the emergence of the group size-cognition relationship in juveniles. However, much like the adults, neither body mass (Pearson's correlation, $r = 0.291$, $p = 0.2$, $n = 21$ individuals tested from 11 groups ranging in size from 3-12) nor latency to interact with the task (Spearman's correlation, $r = -0.144$, $p = 0.532$, $n = 21$ individuals tested from 11 groups ranging in size from 3-12) correlated with group size in juveniles, suggesting there is no difference in motivation between groups (the correlations reported were for juveniles at 100 days post-fledging, but results were qualitatively the same for all ages). Furthermore, body mass and latency to interact with the tasks did not predict cognitive performance when the group size-cognition relationship had emerged at both 200 and 300 days post-fledging (Ashton, Ridley, et al., 2018).

We found strong positive correlations in individual performance across the four tasks in our test battery. On the basis of these findings, Smulders(2018) suggests we "jump to conclusions about general intelligence" in Australian magpies. While we point out the parallels between our results and the literature on "general intelligence", we deliberately avoid the term when discussing our findings and follow Shaw et al.(2015) in using the more neutral term "general cognitive performance". We are also careful to be open about the fact that the underlying causes of correlations between performance on different tasks are not understood (supplementary material: "It is, however, worth noting that the underlying causes of the correlations in performance among tasks are not known. It is, for instance, possible that some performance in all tasks may place similar demands on working memory (e.g. in colour discrimination individuals must not only learn, but remember which colour was rewarded)" Ashton, Ridley, et al., 2018). However, we wholeheartedly agree that expanding the cognitive test battery to include a greater variety of tests covering a wider range of cognitive domains will help elucidate the extent to which Australian magpie cognition is underpinned by domain-general processes (see also Whiten, 2018). The suggestion to test dispersed juveniles is

another excellent idea, although contrary to Smulders' argument, non-territorial flocks of juveniles occur only in the Eastern (non-cooperatively breeding) subspecies of Australian magpie, not in the Western subspecies we studied (Johnstone & Storr, 2004). Likewise, further investigation of the relationship between provisioning rate and female cognitive performance is an important future research objective that will help elucidate the causes and consequences of individual variation in cognition in Australian magpies. However, we reiterate there is no evidence to suggest females in larger groups are more food-motivated, indicating that if a relationship between female cognitive performance and female provisioning rate did emerge, it is likely to be underpinned by cognitive processes.

In summary, as Smulders suggests, the results of observational studies are often open to alternative explanations, but the evidence accumulated from our research provides compelling evidence that, in Australian magpies at least, living in large groups has positive cognitive consequences.

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